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EXPANSION INTO AN HERBIVOROUS NICHE BY A CUSTOMARY CARNIVORE: BLACK-TAILED GODWITS FEEDING ON RHIZOMES OF *ZOSTERA* AT A NEWLY ESTABLISHED WINTERING SITE

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Abstract. In expanding populations, individuals may increasingly be forced to use sites of relatively low quality. This process, named the "buffer effect," was previously described for the Black-tailed Godwit (*Limosa limosa islandica*) in its use of nonbreeding sites in Great Britain and of breeding areas in Iceland. On the basis of diet analyses from droppings and stable isotopes, we describe a new case for the expanding French wintering population of the Black-tailed Godwit, an expansion accompanied by a drastic change in feeding strategy. In the 1990s, Black-tailed Godwits started using intertidal mudflats at Ile de Ré, where they eat the rhizomes of seagrass (*Zostera noltii*) rather than the customary shellfish (*Macoma balthica*) eaten at both the preferred (initial) site (Aiguillon Bay) and the area occupied last (Yves to Marennes-Oléron bays). Individually color-marked godwits appeared faithful to both diet type and site, suggesting a cost of a change of strategy. This represents a first case of rhizome-feeding in shorebirds, and it exemplifies a case of carnivorous birds occupying a new site shifting to herbivory.

Key words: behavioral plasticity, buffer effect, herbivory, seagrass, intertidal flats, shorebirds, stable isotopes.

Expansión a un Nicho Herbívoro por un Carnívoro Tradicional: *Limosa limosa islandica* Alimentándose de Rizomas de *Zostera* en un Sitio de Invernada Establecido Recientemente

Resumen. En las poblaciones en expansión, los individuos pueden verse cada vez más forzados a usar sitios de calidad relativamente baja. Este proceso, llamado "efecto de amortiguamiento," ha sido descripto previamente para *Limosa limosa islandica* en su uso de sitios no reproductivos en Gran Bretaña y de áreas reproductivas en Islandia. Sobre la base de análisis de dieta de excrementos e isótopos estables, describimos a nuevo caso para la población invernal francesa en expansión de *L. l. islandica*, una expansión acompañada de un cambio drástico en la estrategia alimenticia. En la década de 1990, *L. l. islandica* comenzó a usar marismas intermareales en la isla de Ré, donde comen los rizomas del pasto marino *Zostera noltii* más que el habitual marisco *Macoma balthica*, comido tanto en el sitio preferido inicial (bahía Aiguillon) como en el área ocupada luego (bahías Yves hasta Marennes-Oléron). Las aves marcadas individualmente con color parecieron ser fieles tanto a la dieta como al sitio, sugiriendo un costo en el cambio de estrategia. Esto representa un primer caso de consumo de rizomas en aves playeras y ejemplifica un caso de aves carnívoras que ocupan un nuevo sitio cambiando a un hábito herbívoro.

INTRODUCTION

On land the emergence of vascular plants must have favored the expansion of herbivores (Vermeij and Lindberg 2000). By consuming the living plant tissues directly, herbivores short-circuit the pathway to decomposers and thus increase the flow of energy and nutrients. However, plants' low content of energy and high content of fiber require complex and specialized digestive mechanisms, long digestive processes, and large guts (van Soest 1982, Demment and van Soest 1985, Klasing 1998). Therefore, a diet of plants should be relatively difficult to achieve for flying animals such as birds that have to trade a high daily requirement of energy against the cost and ease of flight (Foley and Cork 1992, Klasing 1998, Mackie 2002). Interestingly, making a living on living plants is a dietary specialization that in several different

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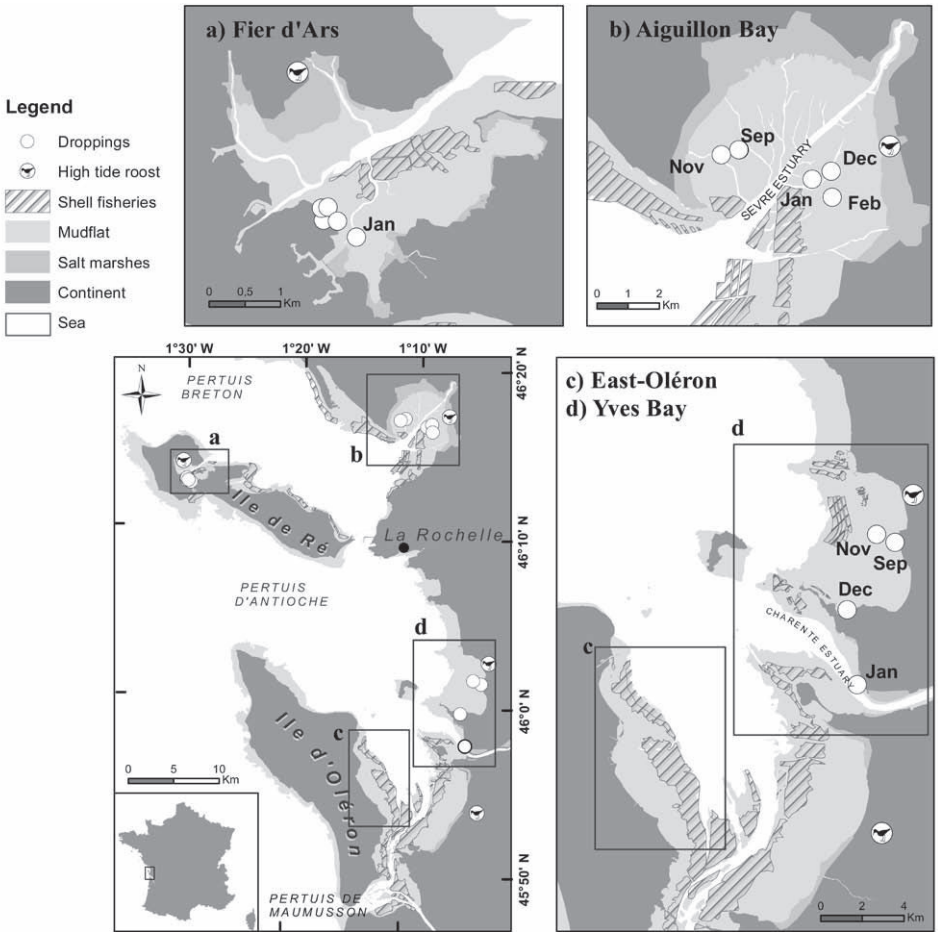

FIGURE 1. Map of the coast of Charente-Maritime and southern Vendée, France, with details of Fier d'Ars on Ile de Ré (a), Aiguillon Bay (b), and Yves Bay/Marennes-Oléron Bay (c). Sites where droppings of the Black-tailed Godwit were collected are indicated with open circles. Circles with bird symbols represent high-tide roosts where godwits were counted and their blood was sampled.

groups of animals was one of the last to evolve (Vermeij and Lindberg 2000, Mackie 2002).

During their annual cycle, birds face density-dependent processes such as resource depletion, interference competition, and territoriality (Sutherland 1996a, b, Goss-Custard et al. 2006). During an increase of the population these processes lead birds to expand into new, but not necessarily the best, areas (Gill et al. 2001, Gunnarsson et al. 2005). By a process termed the regulatory "buffer effect" (Kluyver and Tinbergen 1953, Brown et al. 1996), increasing numbers of birds settle in poor-quality habitats such that lower quality sites "buffer" higher-quality sites. At the same time, expansion into new habitats may favor the emergence of innovative behaviors, including styles of feeding (Greenberg 2003).

Over the last 20 years the population of the Icelandic Black-tailed Godwit (*Limosa limosa islandica*) has increased steeply (Gill et al. 2007). From the early 1990s to 2010, the French wintering population increased sevenfold from 4000 to 27 000 birds (Mahéo 2010), and this has involved the expansion into new wintering sites along the French Atlantic coast. Here we describe differences in the historical changes in the use of three areas in relation to the godwits' site-specific diets. Shorebirds, and certainly the sandpipers (Scolopacidae), usually eat invertebrates (Piersma 2006, Kuwae et al. 2012); Klasing (1998) classified them as "microfaunivores." This is also true for the Black-tailed Godwit (e.g., Moreira 1994, Lourenço et al. 2008), although it feeds extensively on rice kernels as well (Tréca 1984, Lourenço and Piersma 2008). To test if the buffer effect applies to the godwits wintering in France, we here combine count results and observations on site use by individual Black-tailed Godwits with diet analyses, both traditional analyses of droppings as well as stable-isotope analyses.

MATERIAL AND METHODS

This study was carried out along the coasts of southern Vendée and Charente-Maritime, a region known as the Pertuis Charentais (Fig. 1, Verger 2005). Here about a third of

the Icelandic Black-tailed Godwits wintering in France are found (Triplet et al. 2007). One study site is located on the Ile de Ré, the two others are on the mainland coast. On Ile de Ré, the study site is a 719-ha bay enclosed by high dikes (Fig. 1a, 46° 13′ N, 1° 29′ W). A large part of the mudflats is covered with the seagrass *Zostera noltii*. Aiguillon Bay (Fig. 1b, 46° 17′ N, 1° 10′ W) covers 3900 ha and is surrounded by salt marshes and bordered by dikes or cliffs. The upper and middle reaches of the intertidal zone are bare muddy flats, but the lowest parts are criss-crossed by a network of channels. Thirty km further south, Yves Bay, with ~3000 ha of intertidal mudflat, is separated by the Charente River from Marennes-Oléron Bay, with 5500 ha of mudflats wedged between the mainland coast and Ile d'Oléron (Fig. 1c, 45° 57′ N, 1° 05′ W).

All three areas were covered by monthly counts (Caillot and Elder 2000–2009) done while the birds were roosting at high tide (Fig. 1). We estimated densities by dividing counts at roosts by the extent of the intertidal mudflats where the birds feed. On the basis of Wetland International Counts between 1976 and 2010 (done every year in mid-January; Mahéo 2010), we examine the rate of change of the population at each site relative to the total number in France. The slopes of this relationship indicate the rates of filling up in the different areas and thus any buffer effects (Moser 1988, Jackson et al. 2004). In the Yves and Marennes-Olèron part of the system, in the course of the winter godwits tend to move from Yves Bay into Marennes-Oléron Bay, so we define this area as a single unit.

We collected a total of 575 individual droppings at 14 different feeding sites from September 2004 to February 2005 (Fig. 1), then sieved them successively through 300-μm and 64-μm sieves. Black-tailed Godwits ingest bivalves whole (Koolhaas et al. 1993), and fragments of shells are found in droppings (Moreira 1994). We reconstructed the diet from mollusk remains by following Dekinga and Piersma (1993) and from annelid remains by following Scheiffarth (2001). In addition, we collected remains of rhizome fibers from the 300-μm sieve and dried them to constant mass. The diets could then be compared by site on the basis of dry mass.

We also assayed diet type on the basis of the isotopic signal (Hobson and Clark 1992a, b) in whole blood of birds caught at night at high-tide roosts by mist nets. We collected potential prey among the most abundant species in areas where the godwits feed at each site during the period that the birds were there. Prey and blood samples were dried and the dry samples were weighed (0.200 to 0.500 ± 0.001 mg). All samples were placed in tin capsules for analysis of stable isotopes of carbon and nitrogen in an elemental analyzer (Flash EA 1112 fitted with a "no blank" option, Thermo Scientific, Milan, Italy) coupled to an isotope-ratio mass spectrometer (Delta V Advantage, Conflo IV interface, Smart EA option, Thermo Scientific, Bremen, Germany). We report the results as per mil (‰) in the δ unit notation as deviations from standards (Vienna Pee Dee Belemnite for $\delta^{13}C$ and N^2 in air for $\delta^{15}N$), following the formula $\delta = 1000(R_{sample} - R_{standard})$, where δ is the sample's ratio (^{13}C or ^{15}N) relative to a standard (traceable to a primary international standard) and R is the ratio of the heavy to the light isotope ($^{13}C/^{12}$ C or $^{15}N/^{14}N$) in the sample or standard. We report values of $\delta^{13}C$ and $\delta^{15}N$ relative to their primary international standards. The analytical precision of the measurements was <0.06‰ and <0.1‰ for carbon and nitrogen, respectively. In the analysis, we express $\delta^{13}C$ and $\delta^{15}N$ as means ± SD and compared them by a nonparametric Mann–Whitney–Wilcoxon test. We estimated the proportions of prey items assimilated in winter (i.e., October–January; Robin 2011) by a Bayesian approach to mixing models dependent on stable-isotope concentration and computed with 1 million iterations in the package SIAR (Parnell et al. 2010). These models take into account the variability in the prey mixture and the elements' concentration. Here we used the trophic enrichment factor of 1.3‰ for ^{13}C and 2.9‰ for ^{15}N reported for the Dunlin (*Calidris alpina*) by Ogden et al. (2004). Signatures of prey used for the various sites are listed in Table 1.

We examined individual godwits' fidelity to a site by analyzing the resightings of individually color-banded birds. Individuals regularly observed in intertidal habitats in Pertuis Charentais (2006–2009) we categorized by whether they stayed faithful to the initial wintering site or whether they moved to a site where birds were eating different things. To identify whether a birds was feeding as a generalist or specialist, we tested the observed distribution of diet shift with a binomial exact test against a simple null model of random distribution (probability of 0.5 to shift diet or not).

RESULTS

The earliest Black-tailed Godwits wintering in Pertuis Charentais arrived in July, with numbers increasing rapidly in September (Fig. 2). In fall, the birds filled up Aiguillon Bay and Yves/Marennes-Oléron before Ile de Ré, but with more than 4 individuals ha^{-1} in November, Ile de Ré eventually had the highest densities of godwits. Indeed, on the seagrass beds there, godwits occurred in such dense flocks that they looked like the dense flocks of grazing geese. Over the years, with the increase in the numbers wintering in France, Aiguillon Bay a showed small increase in numbers (slope 0.46, Fig. 2), whereas both Ile de Ré and Yves/Marennes-Oléron showed strongly increasing numbers (1.88 and 3.74, respectively; Fig. 2).

On the basis of dropping analyses (Fig. 3), godwits from both Aiguillon Bay and Yves/Marennes-Oléron were eating only molluscs (mainly *Macoma balthica*), whereas the godwits on Ile de Ré had a diet mainly of -rhizomes of *Zostera noltii*. We never found remains of crustaceans. Both large worms (Nereidae) and small worms (Capitellidae and Maldanidae) were rare, accounting for less than 0.5% of the diet.

Isotope values in the whole blood of godwits from Ile de Ré were lower ($\delta^{15}N = 11.7 \pm 1.1$‰; $\delta^{13}C = -12.1 \pm 0.7$‰, $n = 25$) than in that from godwits from Aiguillon Bay and Yves/

TABLE 1. Values of $\delta^{13}C$ and $\delta^{15}N$ (‰) and concentration of elements in potential prey species by feeding area (mean ± SD).

Sites and dates of sampling; species	n[a]	$\delta^{13}C$ Mean ± SD	$\delta^{15}N$ Mean ± SD	$\%^{13}C$ Mean ± SD	$\%^{15}N$ Mean ± SD
Ile de Ré, 46° 12′ 29″ N, 1° 29′ 16″ W, November 2008					
Macoma balthica	3	–13.51 ± 0.15	11.42 ± 0.37	35.03 ± 1.24	9.89 ± 0.34
Scrobicularia plana	3	–13.26 ± 0.43	11.56 ± 0.21	24.67 ± 6.05	6.68 ± 1.95
Cerastoderma edule	3	–12.43 ± 1.03	11.16 ± 1.37	38.50 ± 5.99	11.50 ± 2.15
Ruditapes sp. (siphons)	4	–12.45 ± 0.50	10.60 ± 0.28	41.10 ± 1.93	12.80 ± 0.53
Hydrobia ulvae	3[b]	–10.87 ± 0.38	10.58 ± 1.52	37.12 ± 6.25	10.25 ± 2.46
Small worms (Capitellidae)	3[b]	–13.81 ± 0.45	10.60 ± 0.16	37.67 ± 3.99	10.69 ± 1.69
Zostera noltii (rhizome)	4	–11.53 ± 0.39	7.75 ± 0.76	33.86 ± 1.68	1.64 ± 0.31
Aiguillon Bay, 46° 15′ 52″ N, 1° 9′ 11″ W, February 2009					
Macoma balthica	4	–15.35 ± 0.63	10.60 ± 0.39	40.95 ± 3.08	11.56 ± 1.61
Hydrobia ulvae	3[b]	–13.37 ± 0.12	10.82 ± 0.17	45.80 ± 8.41	12.95 ± 2.42
Scrobicularia plana	3	–15.27 ± 1.05	11.90 ± 0.59	32.36 ± 10.48	9.06 ± 3.77
Large worms (Nereidae)	4[b]	–14.32 ± 0.62	13.78 ± 0.70	37.22 ± 4.15	10.28 ± 1.59
Large worms (Nepthiidae)	4[b]	–15.02 ± 0.50	15.14 ± 0.23	28.58 ± 4.16	8.02 ± 1.34
Yves Bay, 46° 0′ 32″ N, 1° 3′ 29″ W, November 2008					
Macoma balthica	3	–14.69 ± 0.18	10.30 ± 0.61	35.45 ± 3.55	10.17 ± 1.35
Hydrobia ulvae	3[c]	–11.77 ± 0.21	10.06 ± 0.11	40.43 ± 1.53	11.43 ± 0.54
Scrobicularia plana	3	–14.23 ± 0.70	10.32 ± 0.13	33.40 ± 5.73	9.70 ± 1.92
Marennes–Oléron Bay, 45° 56′ 5″ N, 1° 5′ 2″ W, January 2009					
Macoma balthica	3	–13.91 ± 0.10	9.81 ± 0.24	41.36 ± 1.17	11.80 ± 0.86
Hydrobia ulvae	3[c]	–11.44 ± 0.28	10.30 ± 1.16	41.39 ± 0.89	11.90 ± 0.17

[a]Number of samples; each sample was in general composed of one individual but for small species we combined for analysis.
[b]5 individuals.
[c]10 individuals.

Marennes-Oléron ($\delta^{15}N$ = 13.4 ± 0.8‰; $\delta^{13}C$ = –13.4 ± 13.5, n = 80) ($\delta^{15}N$, U = 179.5, P < 0.001; $\delta^{13}C$, U = 1813, P < 0.001). At Ile de Ré, *Zostera* had the value of $\delta^{15}N$ lowest (7.7 ± 0.8‰) and value of $\delta^{13}C$ highest (–11.5 ± 0.4‰) of all the local sources (Fig. 4). Actually, the godwits that grazed on rhizomes there had the same levels of $\delta^{15}N$ as in the bivalves they ate elsewhere. The contribution of *Zostera* to the diet as estimated from mixing model was 26.5 ± 5.3%, with 10.7 ± 10.2% for bivalves (Scrobiculariidae) and 62.8 ± 5.3% for small worms (Fig. 3). The mean signatures of $\delta^{13}C$ and $\delta^{15}N$ in birds matched those in their main prey at each site as characterized by the contents of droppings. At the sites where godwits fed on *Macoma*, the mixing model attributed its contribution as 44.3 ± 14.3% at Aiguillon Bay and 96.6 ± 2.7% at Yves/Marennes-Oléron Bay (Fig. 3).

We found that only 24 ± 12% of the individual Black-tailed Godwits observed at Ile de Ré early in winter were later observed at sites where they would have shifted to a diet of mollusks (2006–2007, n = 3/23 individuals; 2007–2008, n = 3/14; 2008-2009, n = 15/40; Table 2). Conversely, godwits that were first observed at sites with molluscan prey were almost never resighted at Ile de Ré later in the winter (Table 2, n = 2/108). In contrast, there were many exchanges between sites where godwit fed on mollusks, e.g., the movements between the Yves and Marennes-Oléron roosts observed in 96 ± 2% of birds (Table 2; these individuals maintained a diet of bivalves).

DISCUSSION

Recently, stable-isotope analyses have been put to good use to assay the diets and habitat use of shorebirds (Ogden et al. 2005, Kohler et al. 2009, Dietz et al. 2010). Here we demonstrated the eating of rhizomes by some Black-tailed Godwits but not others, and isotope analyses confirmed the assimilation of this plant material. Herbivory (rather than the granivory of rice-eating godwits and the Ruff [*Philomachus pugnax*]) has been reported in only two other species of shorebirds, and both godwits, the Hudsonian (*Limosa haemastica*) and Marbled (*L. fedoa*) Alexander et al. (1996) reported those species feeding on tubers of *Potamogeton pectinatus* during their spring migration in North America.

Kuwae et al. (2008) has shown than small species of shorebird may feed directly from algal biofilm on the surface of an intertidal mudflat, and Kuwae et al. (2012) revealed that direct predator–prey relationship between shorebirds and biofilm are widespread and mediated by multiple ecological and evolutionary determinants. Our study confirms that even large shorebirds feed directly on plants in marine systems.

Estimating diet content by the dry mass of remains might lead to a bias in term of energy intake for each type of prey. However, considering the limited information on

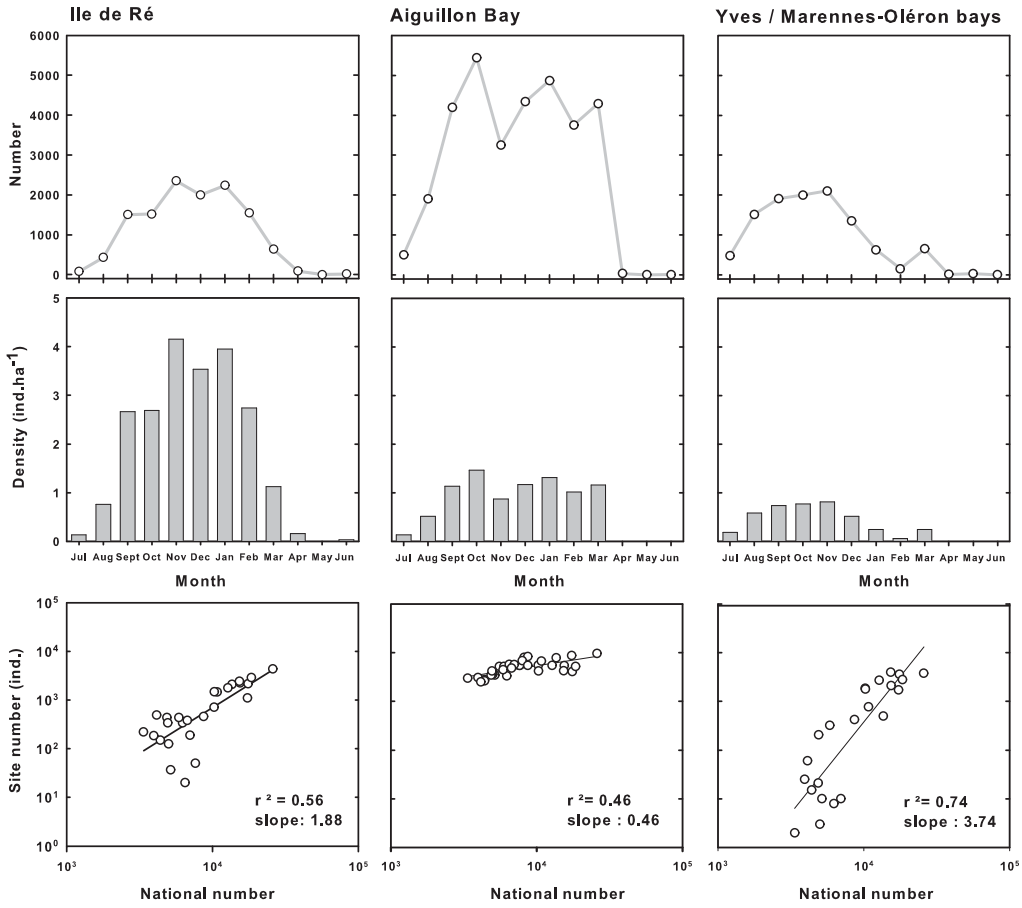

FIGURE 2. Numbers of the Black-tailed Godwit (top row), its density at each site (middle row) during the nonbreeding season of 2004–2005 in the three areas where it winters in the Pertuis Charentais, France, and the degree to which the three sites filled up as the population wintering in France increased (bottom row). In the bottom row, numbers recorded at each site are plotted as a function of the national count (mid-January counts from 1976 to 2010, from Mahéo 2010). The rate of change at each site was calculated as the slope of the linear regression line (log 10).

fiber digestibility, search efficiency, and handling time by the herbivorous godwits, estimates based on dry mass yield the best values for comparisons. Stable-isotope analyses of whole blood established conclusively that the godwits assimilated material from the rhizomes. Nevertheless, their contribution to the diet (Fig. 3) could be underestimated, as in the mixing model we were obliged to enter bivalves (*Scrobicularia*) and small worms at the same mass as *Zostera*. In reality, rhizomes may have been ingested accidentally, as is suggested by the finding that microscopy revealed no worms in the droppings of these rhizome-eaters at Ile de Ré. When worms are excluded from the mixing model, the contribution of *Zostera* grows to 94.3 ± 1.0 % of the diet. Similarly, the contribution of *Macoma* to the diet in the birds eating mollusks could also be underestimated (see Robin 2011). Such underreporting would not change the story, however.

Resightings of individually banded Black-tailed Godwits showed that they were more faithful to feeding style and diet than to their precise wintering site. Four godwits at Ile de Ré with an isotopic signature characteristic of bivalves rather than of *Zostera* must have been birds in transit; intermediate values were absent (Fig. 4). That godwits show such individual diet specialization may be explained by rhizomes and hard-shelled bivalves requiring distinct digestion-related adjustments to the gut. Whereas the feeding on tubers induces a long digestive tract, long digestive pauses, and particular digestive juices (Klasing 1998), birds ingesting mollusks whole need strong gizzards for crushing prey (van Gils et al. 2003, 2006, Battley and Piersma 2005). Nevertheless, in 2007–2008 three out of 14 individuals, and in 2008–2009 15 out of 40 individuals, appeared to have made the shift from eating rhizomes to eating bivalves in the course of the winter (Table 2). We suggest this is due to the depletion of seagrass (Inger et al.

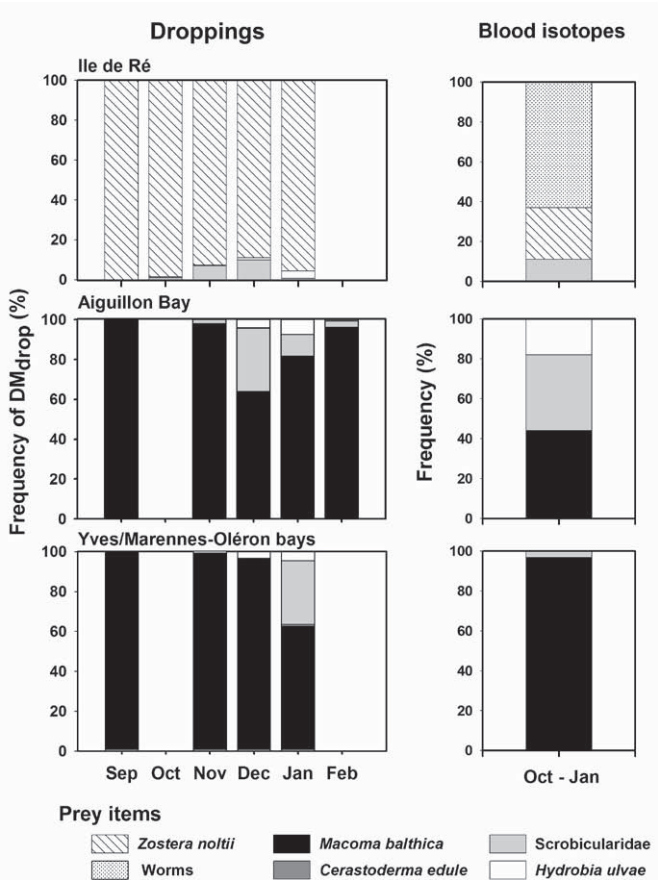

FIGURE 3. Composition by month of reconstructed diets of the Black-tailed Godwits at Ile de Ré, Aiguillon Bay, Yves/Marennes-Oléron bays, expressed as the percentage of dry mass of remains in droppings (DM_{drop}) from September 2004 to February 2005. Diets were based on 25 pooled droppings at Ile de Ré and 50 pooled droppings at the other two sites each month. For each site, the fraction of prey in whole blood is expressed for October–January (2007–2009) from the mixing model of stable isotopes for 25 birds from Ile de Ré, 6 birds from Aiguillon Bay, and 161 birds from Yves/Marennes-Oléron.

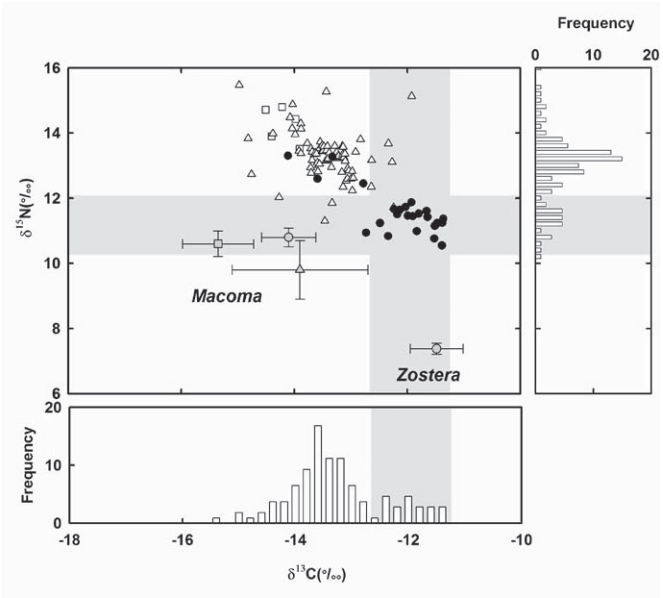

FIGURE 4. Distribution by site of $\delta^{13}C$ and $\delta^{15}N$ (‰) in whole blood sampled from Black-tailed Godwits in winter (October–January 2007–2010). Godwits sampled at Ile de Ré are represented by filled circles, at Aiguillon Bay by open squares, and at Yves/Marennes-Oléron by open triangles. Solid gray symbols are the mean values at each site for the bivalve *Macoma balthica* and the mean value for rhizomes of the seagrass *Zostera noltii*.

TABLE 2. Changes in the diet of Black-tailed Godwits resighted through the winter. Diet was assigned according to site and the behavior of flock mates during the winters 2006–07, 2007–08 and 2008–09. Deviations from random use of both resources at the end of the winter, regardless of the diet observed at the start of the winter, tested with exact binomial tests.

	Diet at end of the winter			
Diet at start of the winter	*Zostera*	Bivalves	*P*	*n* total
2006–2007				
Zostera	39%	6%	<0.001	51
Bivalves	0%	55%	<0.001	
2007–2008				
Zostera	13%	3%	0.057	85
Bivalves	0%	84%	<0.001	
2008–2009				
Zostera	17%	8%	0.047	145
Bivalves	1%	73%	<0.001	

2006, Nolet et al. 2006). Although the two different diet types both lead to heavy muscular stomachs, a shift from rhizomes to bivalves would easier than the reverse (Piersma et al. 1993). This may be due to the longer retention times expected for birds eating fiber-rich food rather than hard-shelled prey.

Just as predicted by the "buffer effect" demonstrated by Gill et al. (2001), as the population in France increased, two new sites filled up and at one of those the "displaced" birds started to feed on rhizomes in a bed of seagrass without *Macoma*. Obviously, there may be reasons other than diet quality to explain the choice of Ile de Ré, which is settled even before Yves/Marennes-Oléron, where birds eat bivalves (Fig. 2). In midwinter, the coastal wetlands of France are often disturbed by hunters. When the totally protected area at Aiguillon Bay became filled up, godwits were left with a choice between the coastline of Yves/Marennes-Oléron disturbed by hunters (here the godwits can feed on bivalves but have to commute 7 km to suitable and safe roosting sites, Fig. 1) and the undisturbed area at Ile de Ré (necessitating rhizome feeding, but the roost site is only 1 km away). Some

individuals, perhaps the most innovative ones, opted for Ile de Ré. Further studies are now necessary to show whether the energy balances of Black-tailed Godwits at the three sites differ (cf. Quaintenne et al. 2011).

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